THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 10. NOTES ON TWO SPECIES OF MARCGRAVIA

RICHARD A. HOWARD

THE TYPE GENUS *Marcgravia* of the Marcgraviaceae is familiar to collectors in the American tropics for its conspicuous heteroblasty and for the development of pedicellate saccate nectaries at the apex of the dense racemose inflorescence, the flowers of which usually form a distinctive umbel-like cluster. The plagiotropic juvenile shoots of all species of *Marcgravia* examined in the West Indies have distichous leaves arranged on flattened stems which spread over the ground, over and on boulders, and up the trunks of trees (FIGURE 1). Although the juvenile leaves vary in form and size, they have characteristics which permit them to be identified with particular species. In most species the juvenile leaves are subsessile and often overlap the stem (FIGURE 1a). Numerous adventitious roots develop in rows from the stem beneath the leaves and afix the young shoot to the substratum (FIGURE 1b). Sir Hans Sloane in 1707 illustrated the climbing shoots and indicated that they were sterile and that he was unable to associate them with known plants. He listed them with ferns and aroids. With increasing age and with unknown factors of maturity, freely arching orthotropic branches lacking adventitious roots develop from the axils of the juvenile leaves (FIGURE 1c). These axillary stems bear leaves of entirely different size and shape. The apex of the climbing juvenile shoot may also change suddenly, or with transitional phases, to the production of leaves of the mature form, usually when freed by weight or other forces from the substratum. The terminal free shoot or the axillary branch may, upon contact with the trunk of a tree or other substrata, revert to the juvenile leaf form. Examples have been found, and even reproduced in a greenhouse, of the repeated transfer of a single stem from juvenile to mature form and back again (FIGURE 1d).

Stems of *Marcgravia* may reach the canopy of an elfin forest and extend over the crowns of other plants or ascend the trunks of forest trees, forming masses in the branches of the crown, and produce long axillary shoots, pendent or reaching nearly to the ground.

The inflorescence of species of *Marcgravia* in the West Indies is developed terminally on the axillary branches. After flowering and producing fruit, the flowering branch may die back a few internodes before an axillary bud on the same branch develops into a new shoot, continuing the elongation of the primary axis. The apical meristem of *Marcgravia* is surrounded and protected by overlapping leaves which form a slender pointed bud, enlarged at the base (FIGURE 3a). In primordial stages the leaf is terminated by a relatively large multicellular gland often conspicuous in the terminal bud (FIGURES 2c, 4c, 5c). Similar glands may be found along the margin of the lamina (FIGURE 2c). These glands are con-

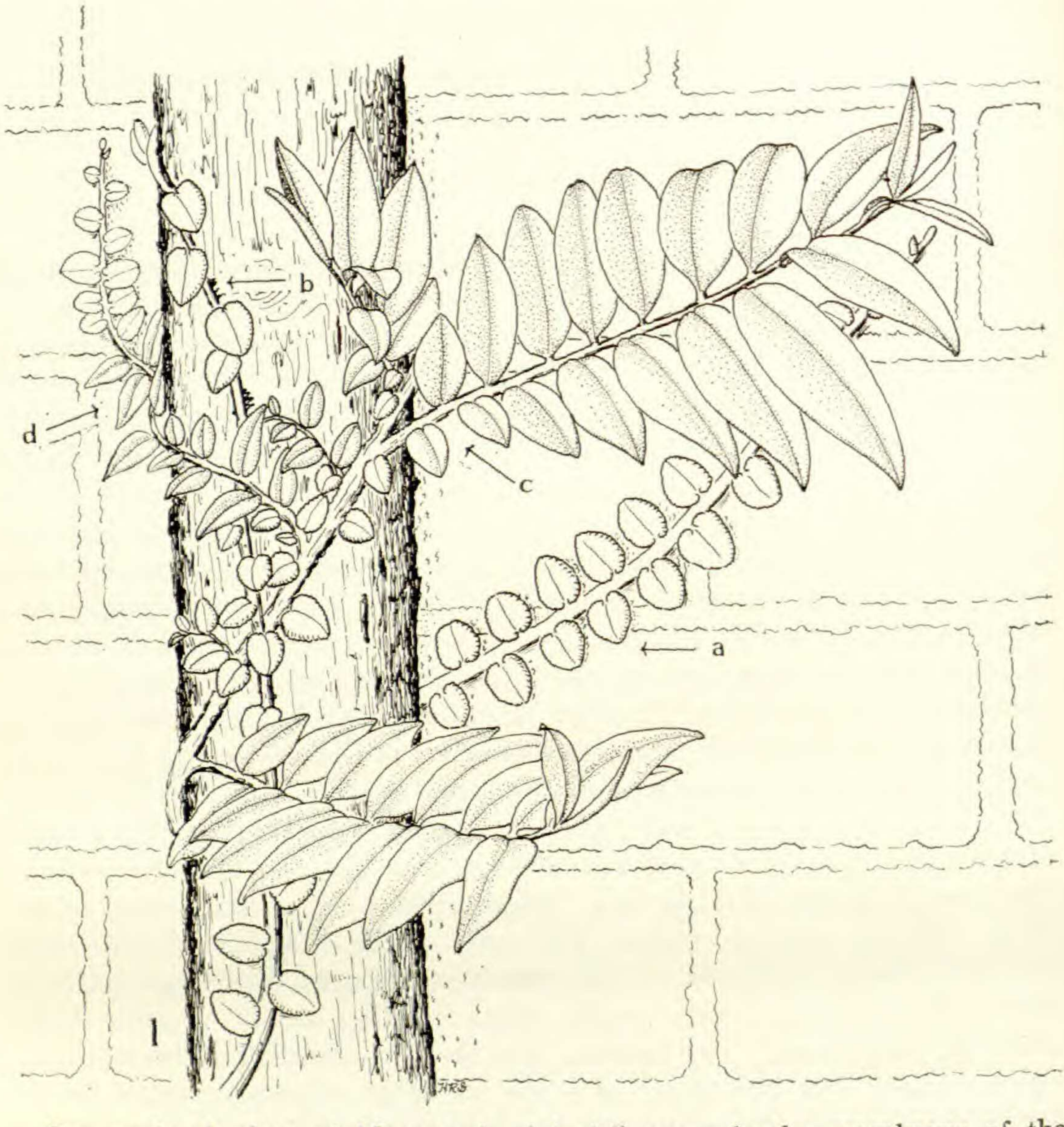
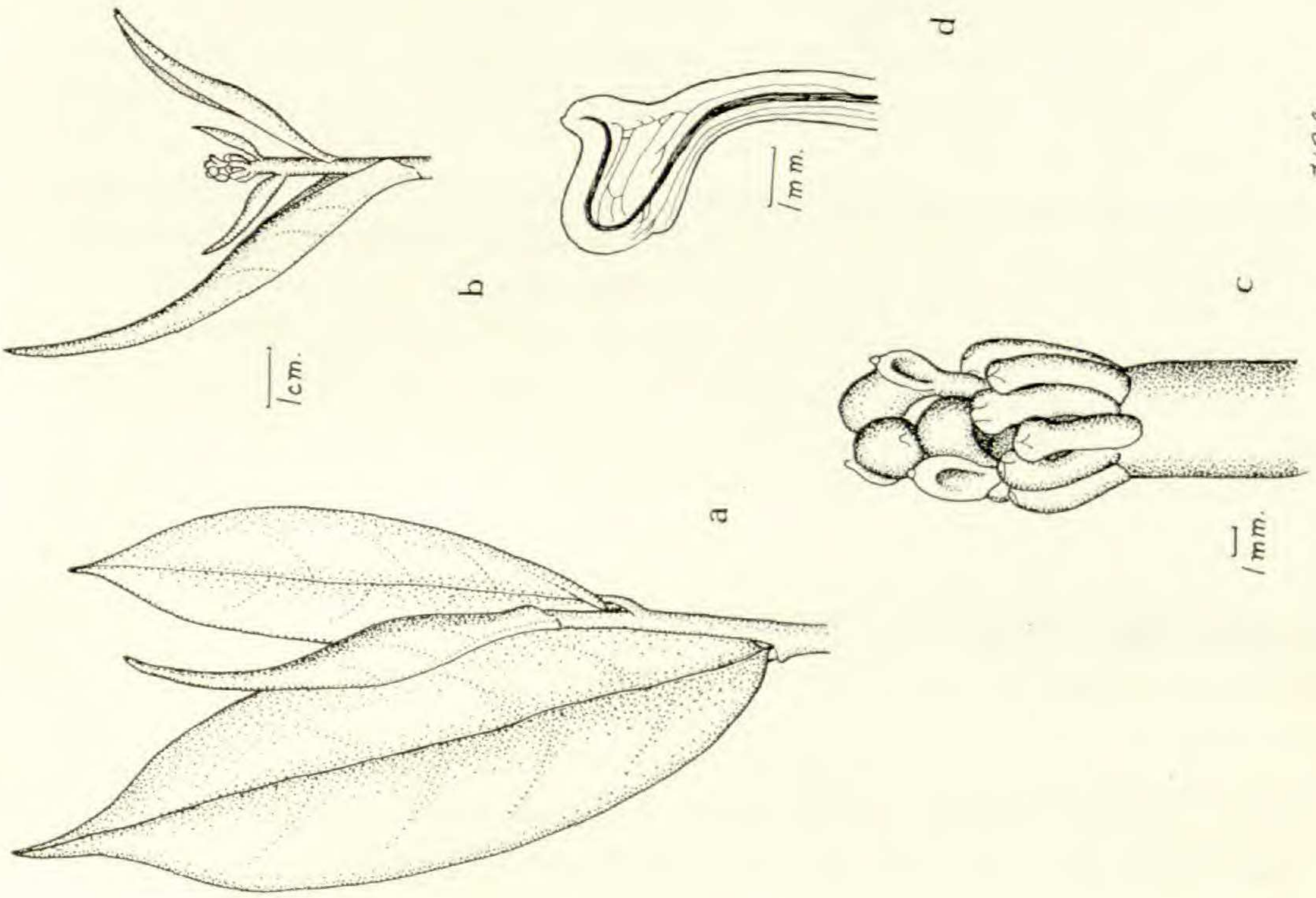


FIGURE 1. A plant of *Marcgravia sintenisii* grown in the greenhouse of the Arnold Arboretum in Jamaica Plain, Massachusetts. a. Plagiotropic stem with juvenile leaf-form appressed to brick wall of greenhouse. b. Adventitious roots of plagiotropic stem visible where leaf has been removed. c. Axillary orthotropic stem showing abrupt transition from juvenile leaf form to adult leaf form. d. An orthotropic stem which changed from the basal juvenile leaf form to the adult leaf form and reverted to the juvenile leaf form on plagiotropic stems when appressed to the wall.

FIGURE 2, left. *Marcgravia sintenisii*. a. Orthotropic stem apex with flower bud. b. Leaves removed to show young inflorescence. c. The inflorescence is a raceme. The nectary-bearing pedicels are contiguous with the flowering pedicels at this stage of development. Marginal hypophyllous glands are shown on the leaf. d. Young flower bud showing large marginal glands of the incipient perianth parts. e, f. Cleared nectaries. g. Two young nectaries showing the aborted flower bud.

FIGURE 3, right. *Marcgravia rectiflora*. a. Orthotropic stem apex with flower bud enclosed in leaves. b. The young inflorescence with nectary-bearing pedicels clearly differentiated at the apex of the raceme. c. The young inflorescence. d. A cleared young nectary showing the early stages of invagination and distortion.



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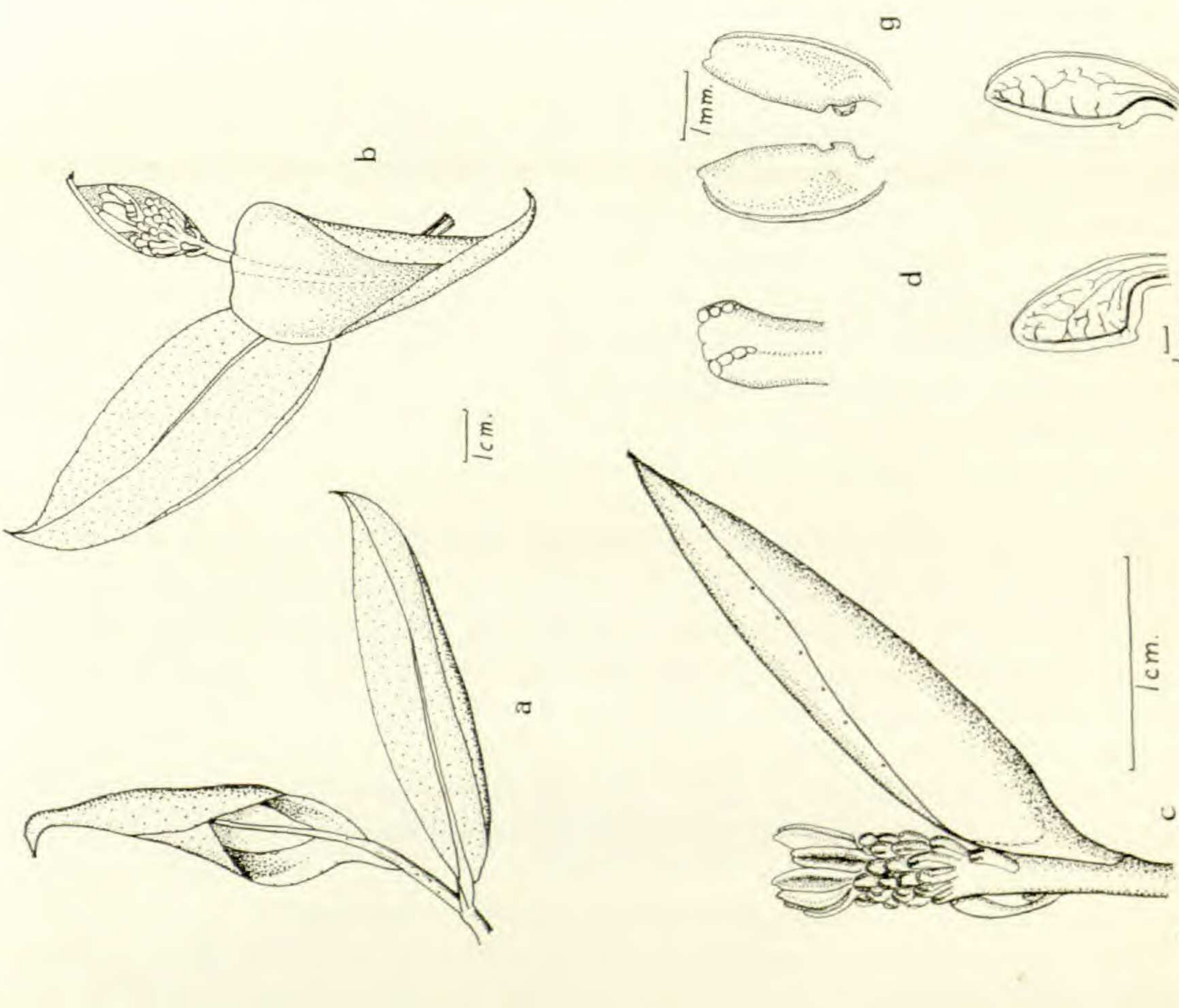

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spicuous in the juvenile leaf form and appear to remain functional for a long period of time. In the adult leaf form the terminal and marginal glands become brown and hard at an early stage of development. Large hypophyllous glands are found in characteristic patterns on the leaf blade, associated with the midvein or localized in particular spots on the lamina (FIGURES 4, 5).

The terminal bud containing a young inflorescence is only slightly more swollen initially than the vegetative bud. There is only a slight reduction in leaf size immediately below the inflorescence. In the raceme the flowering pedicels are borne in a dense spiral, but the axis is terminated with the development of pedicels dominated by the lateral saccate nectary which has its orifice at the base (FIGURES 2c, 3c). The development of the terminal nectary-bearing pedicels is precocious in comparison with the flowering pedicels. The flowering pedicels are ascending in relation to the axis in the young buds and the flowers are borne apically on the pedicel. With continued development the flowering pedicels tend to diverge from the inflorescence axis, in some species to a 90-degree angle, or even to become slightly reflexed. The apical flower primordium retains the same axis as the pedicel in the subgenus ORTHOTHALAMIUM (Wittmach, 1878). In other species forming the subgenus PLAGIOTHALAMIUM the flower bud is offset from the apex and may be at a 90-degree angle to the axis of the pedicel.

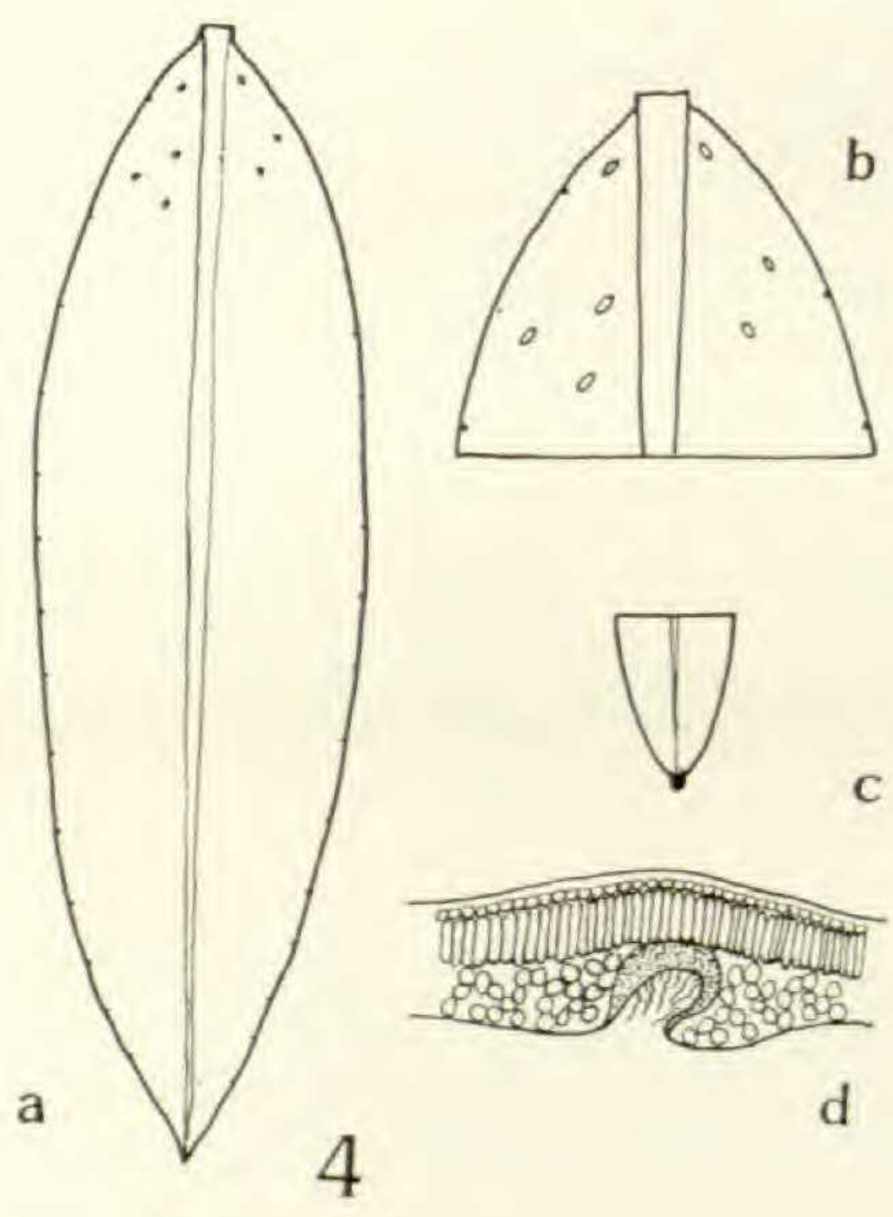
In many species, as in *Marcgravia rectiflora*, the flowering axis remains erect and the flowers ascend (FIGURE 6). The terminal nectary-bearing pedicels, therefore, recurve to varying degrees so that the basal opening of the nectary is oriented upward. In other species, as represented by *Marcgravia sintenisii*, the inflorescence axis is pendent so that the flowering pedicels form an umbel with the flowers pointed downward (FIGURE 7). The axis of the nectary-bearing pedicels, therefore, is not distorted and the basal opening of the nectary is directed upward. This is the characteristic "wheel" of hanging flowers so frequently illustrated as typical of *Marcgravia*, which has given rise to suggestions and speculations that the plants are pollinated by humming birds hovering beneath the open flowers and becoming dusted with pollen while obtaining nectar from the saccate ovaries.

Within the many species of *Marcgravia* nectary-bearing pedicels show considerable variation. The nectary may be nearly as long as the pedicel and is then often described as sessile, or it may range from three-fourths to only one-fourth the length of the pedicel. The majority of species have elongate cylindrical nectaries with an asymmetrical orifice and lip, a narrowed neck, and a swollen base. A few species have flattened and broadened nectaries, described as galeate but to be considered so only when the inflorescence axis is ascending. The terminal pedicels producing nectaries may also bear a minute or abortive flower, suggesting that they are but modifications of the lower, nectary-less, flowering pedicels.

The nectary-bearing pedicels do not persist long after the flowers have shed their calyptrate corollas. No fruiting specimens were found in the

wild or in herbarium collections with the nectary-pedicels remaining attached. Since the shape of the nectary is a character of taxonomic importance, the need for collections of flowering material is apparent.

The morphology of the nectary and its role in pollination are controversial and still undetermined in the available literature for many of the species. Additional field observations are needed. Patrick Browne, in *The Civil and Natural History of Jamaica*, published in 1756, observed on *Marcgravia* that "this curious plant is frequent in the woods of *Jamaica*; and appears in such various forms, that it has been often mistaken for different plants, in the different stages of growth." Of the inflorescence he reported, "The flowers are sustained by long foot-stalks, and disposed in the form of an *umbella*, about the extremities of the branches; but the summit, or crown of the supporter, is constantly adorned with four, five, or more hollow, divergent, glandular bodies, that occupy the center of the *umbella*: these are of an arched oblong form, obtuse and roundish; they are hollow within, and affixed by very short foot-stalks, that rise immediately from one side of the aperture, or opening of the gland; which is



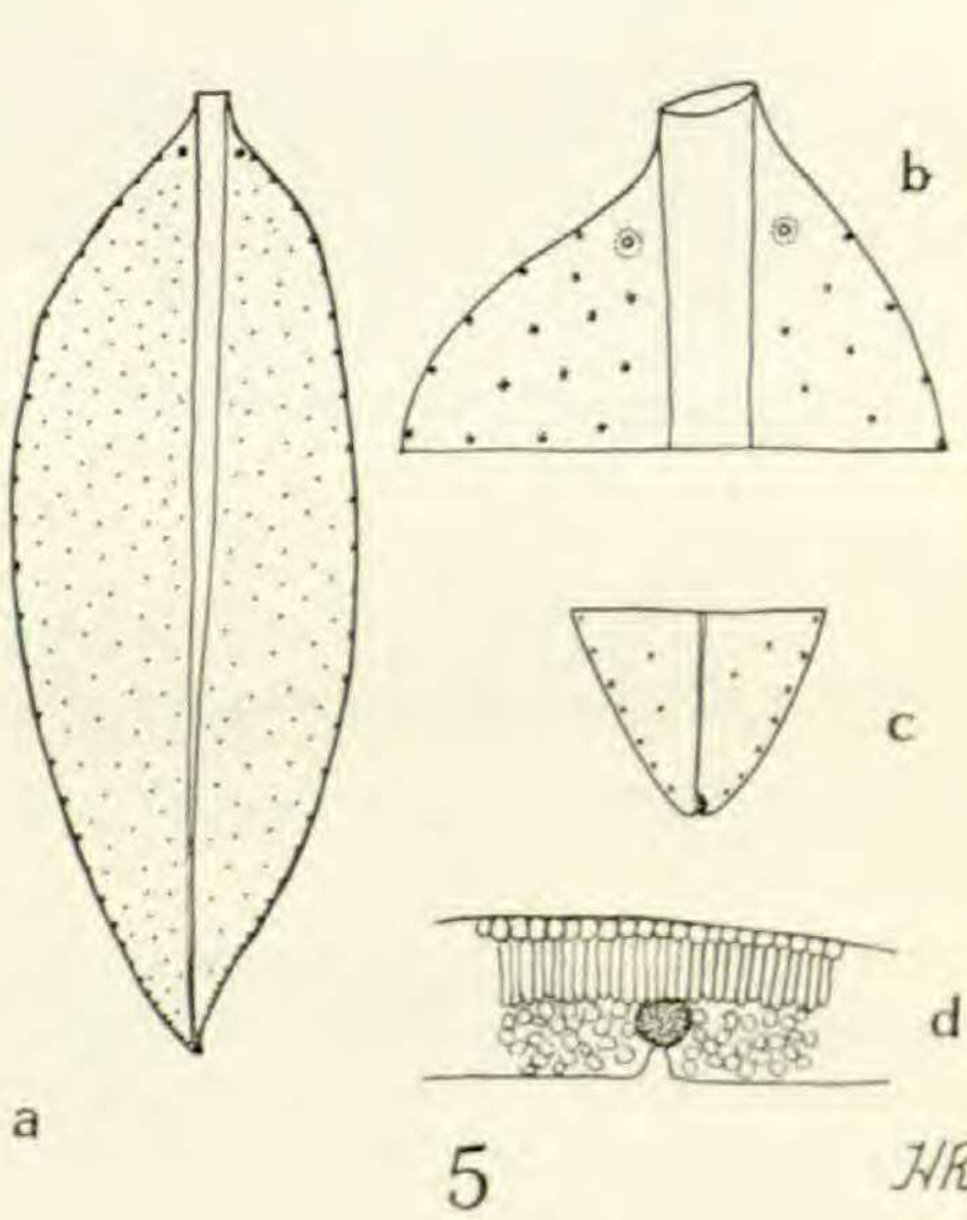


FIGURE 4, left. a, b. Leaf of *Marcgravia sintenisii* showing the several hypophyllous glands near the base of the lamina. c. The terminal gland of young leaf. d. Diagrammatic section of the leaf blade through a gland.

FIGURE 5, right. a, b. Leaf of *Marcgravia rectiflora* showing the two large glands near the base of the lamina. c. Apex of young leaf. d. Diagrammatic section of the leaf blade through a gland.

so disposed, as to receive the water that dribbles down along the branch in rainy weather. What the real use of these may be, is not easily determined: it is, however, remarkable, that the leaves of the branches are plain, of an oblong oval form, with a smooth membranous edge; while those of the younger plants are always observed to have many little glands, set gradually round the margin."

Thomas Belt, author of *The Naturalist in Nicaragua*, published in 1874,

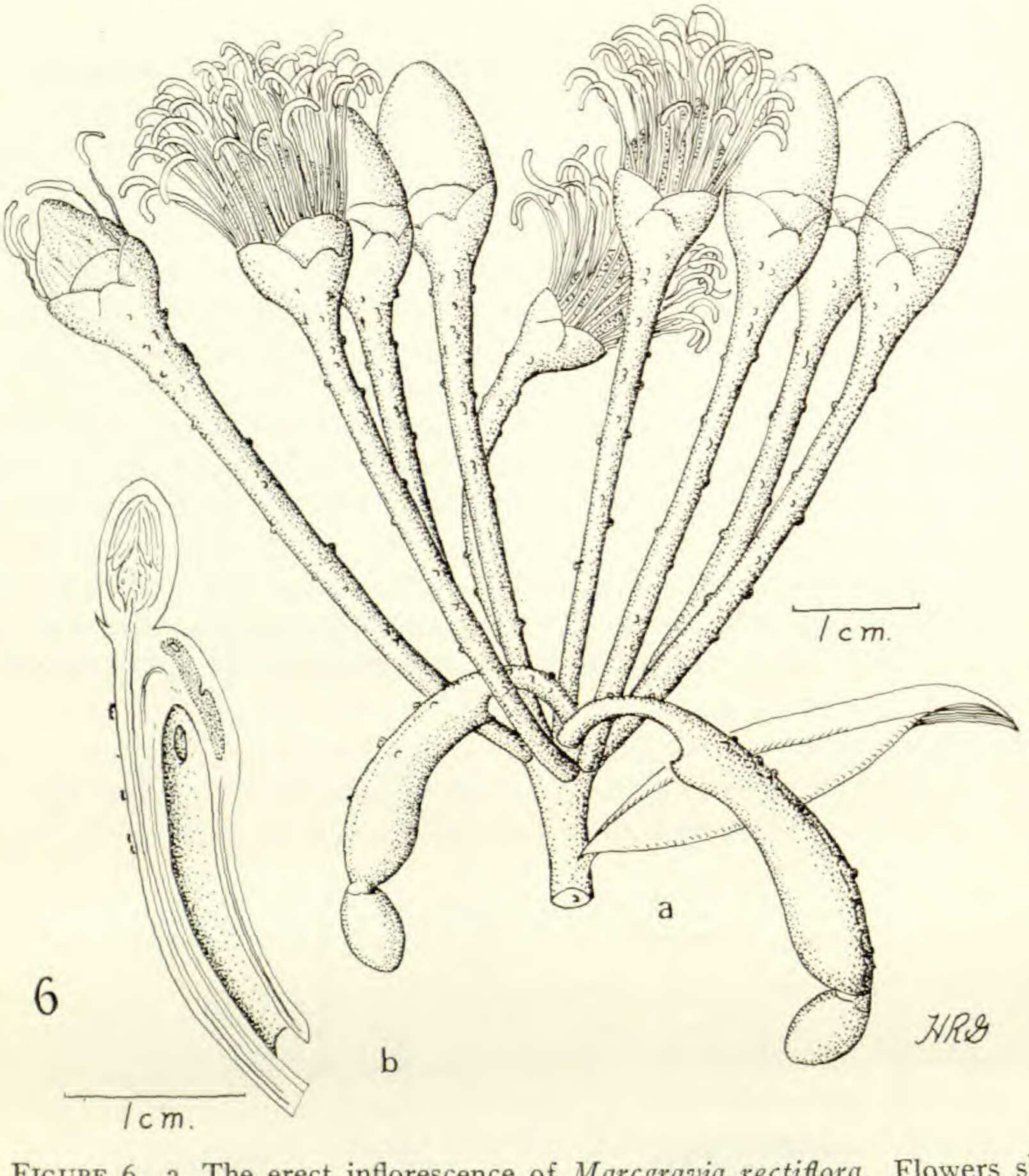


FIGURE 6. a. The erect inflorescence of *Marcgravia rectiflora*. Flowers show the two bracts subtending a four-parted calyx, the calyptrate corolla, and the numerous stamens which have shed pollen before the fall of the corolla. The elongate nectaries are on terminal but recurved pedicels. In this clone the flower bud of the nectary-bearing pedicel has not aborted, but does not mature. b. Diagrammatic representation of the nectary-bearing pedicel. The area of glandular tissue and one of the two pores is shown. The unaltered bract comparable to the modified nectary bract is also shown.

is considered to be the originator of the humming-bird pollination legend. He reported of *Marcgravia nepenthoides*, "The flowers of this lofty climber are disposed in a circle, hanging downwards, like an inverted candelabrum. From the centre of the circle of flowers is suspended a number of pitcher-like vessels, which, when the flowers expand, in February and March, are filled with a sweetish liquid. This liquid attracts insects, and the insects numerous insectivorous birds, including the species I have mentioned and many kinds of hummingbirds. The flowers are so disposed, with the stamens hanging downwards, that the birds, to get at the pitchers, must brush against them, and thus convey the pollen from one plant to another.

A second species of *Marcgravia* that I have found in the woods around Santo Domingo has the pitchers placed close to the pedicels of the flowers, so that the birds must approach them from above; and in this species the flowers are turned upwards, and the pollen is brushed off by the breasts of the birds." This story has been rewritten, applied to other species without verification in many subsequent volumes, although most recently qualified by Meeuse (1961) who states, "In all likelihood birds are the normal pollinators in *Marcgravia*, although bat pollination is suspected in a few cases." A paper by I. W. Bailey (1922) entitled "The pollination of *Marcgravia*: a classical case of ornithophily?", which questioned the general acceptance of humming-bird pollination, has been generally overlooked. Bailey examined several species of *Marcgravia* in British Guiana and concluded the flowers are self-fertile or autogamous, instead of being protandrous and cross-pollinated by birds. He found that inflorescences would set fruit when enclosed in protective cloth which excluded any birds, and he reported that other inflorescences produced fruit under water.

During a recent period of field study in eastern Puerto Rico two species of *Marcgravia* representing the two subgenera and matching the types described by Belt were available in quantity for frequent observation. One species endemic to Puerto Rico, *Marcgravia sintenisii* (FIGURE 7), occurs frequently at higher elevations in the Luquillo Mountains and was in the Pico del Oeste study area (Howard 1968). A second species, *Marcgravia rectiflora* (FIGURE 6), has a wider range of distribution including Cuba and Hispaniola, and is reported from South America; it occurs at a lower elevation in Puerto Rico, primarily along the Rio Cubuy in the Luquillo Mountains.

The species may be contrasted in other ways. *Marcgravia sintenisii* occurs in and on the canopy of the elfin forest. It has a pendent inflorescence developed at the apices of short axillary branches. The flowers, therefore, hang and the stamens are exposed from below. The nectaries are flattened and galeate in normal position but appear flat-topped at the orifice and obtuse at the base, as observed in the flowering condition (FIGURE 7d). The nectaries are pale yellow-orange in color until the corolla cap is ready to break free, when they turn a brilliant red. The flowering pedicels number 30 to 60 and the nectary-bearing pedicels about nine to eleven. The corolla caps fall in the early morning hours and the stamens diverge from the pistil by adaxial growth or elongation. The stigma appeared to be receptive, i.e., glistening and dusted with pollen at the time of abscission of the corolla cap, and within an hour or two after opening the anthers had shed all pollen and begun to wither. The flowers did not mature in sequence according to their position on the axis, but one radial group appeared to shed the corollas, followed by another segment often separated from the first by flowers slower in development. The whitish filaments persisted but were easily dislodged at this stage. Although it appears that the flowers are pollinated in bud, the inflorescence as a whole had still unopened flowers at the same time other flowers had already lost their stamens. In the course of observations made over a period of three

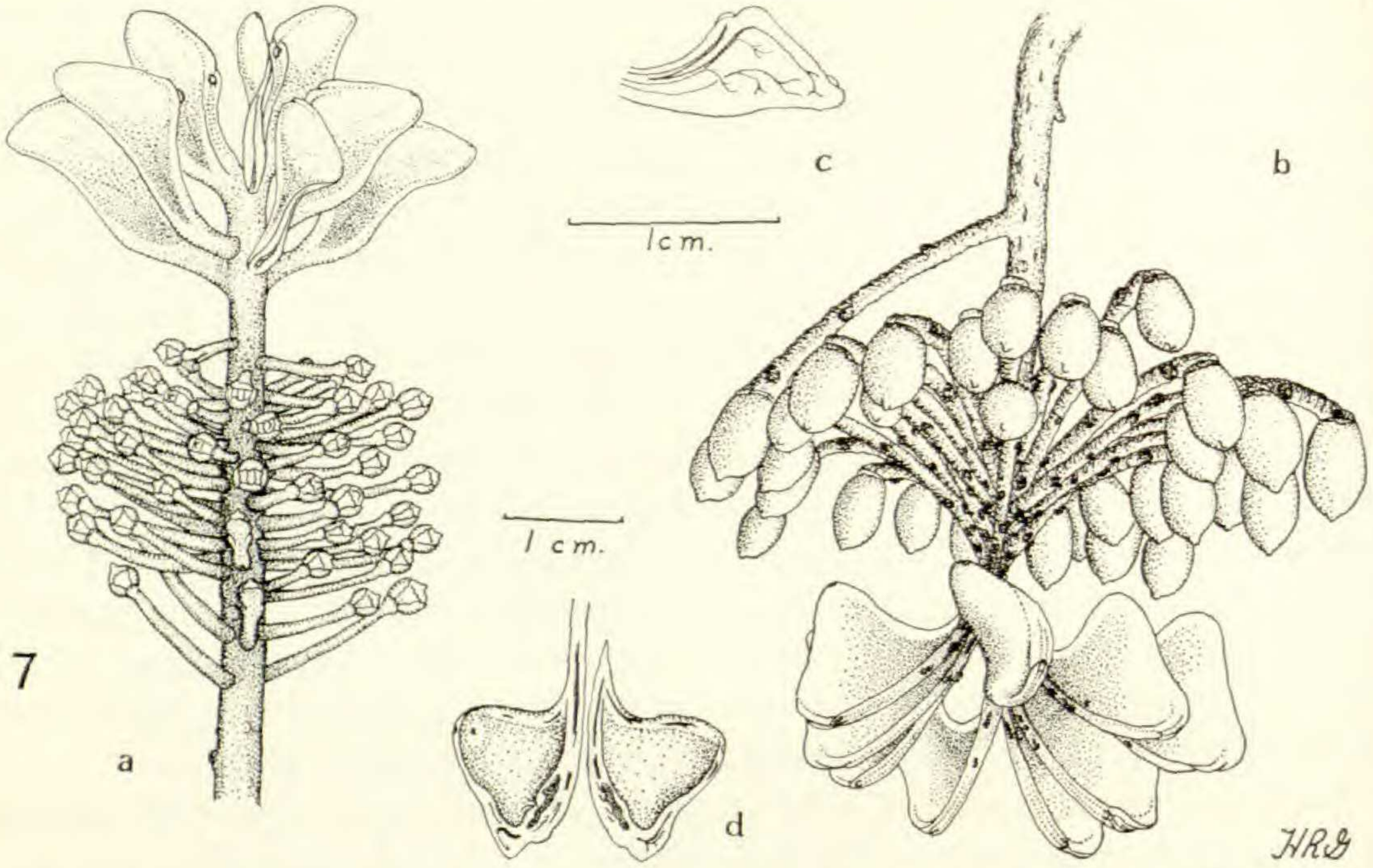
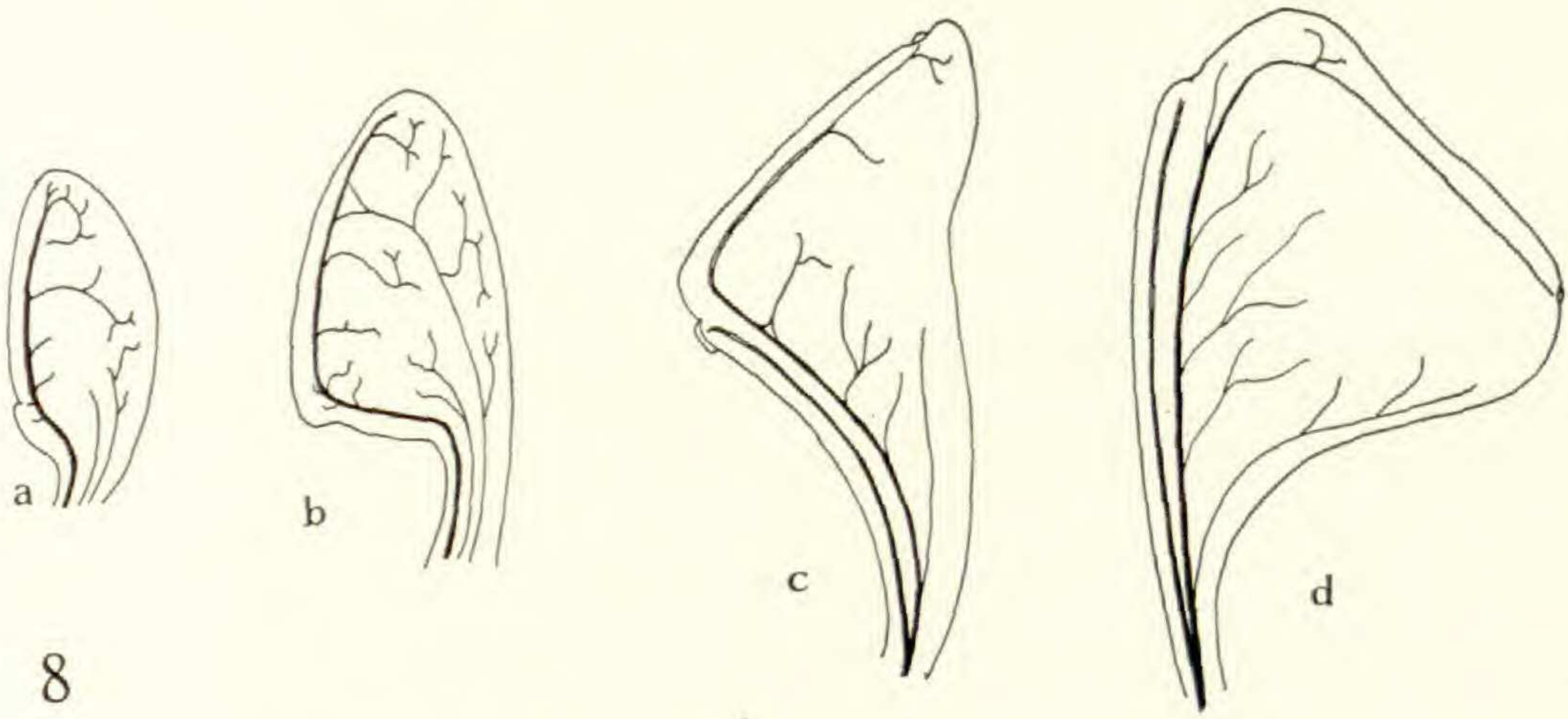


FIGURE 7. *Marcgravia sintenisii*. a. A young erect inflorescence showing the elongation of the axis between the flower-bearing pedicels and the nectary-bearing pedicels. The young flower buds are oriented with the axis of the pedicel. Aborted flower buds are shown on the nectaries. b. The mature inflorescence is pendent. The angle of the flowering pedicels has been altered in development and the flower is now at right angles to the axis of the pedicel. Further shift in orientation of the nectary is evident. c. Diagram of cleared young nectary showing the aborted flower bud. d. The inverted galeate nectary split to show the glandular tissue.

years we noticed that the inflorescences were visited by the green-throated hummingbird (*Sericotes holosericeus*), by Todies (*Todus mexicanus*), and by bees seeking nectar from the orifice of the nectary. The most frequent visitor, however, was the bananaquit (*Coereba flaveola*) which grasped and hung from the brilliantly colored nectaries and pecked at the base (morphological apex) creating sizeable holes in and through the tissue of the nectary. Subsequently the bees also visited these injured areas instead of approaching the nectaries at the natural orifice.

Marcgravia rectiflora is a stronger climbing plant of greater volume, which does not reach the canopy of the forests of lower elevations but seems to dominate many of the host trees by growing luxuriantly on the lower branches. The lateral branches of this species are exceedingly long and pendent, some reaching 15 feet and showing as many as 25 inflorescence scars. The inflorescence in *Marcgravia rectiflora* also develops terminally, but instead of hanging the tips of the branches turn upwards (FIGURE 6). The raceme, therefore, is morphologically erect and the flowering pedicels ascending. The nectaries developed on the terminal pedicels are strongly recurved and hang between the flower-bearing pedicels so that the opening of the nectary points skyward. The nectaries of *Marcgravia rectiflora* are elongate saccate structures larger at the base than at the orifice and nar-



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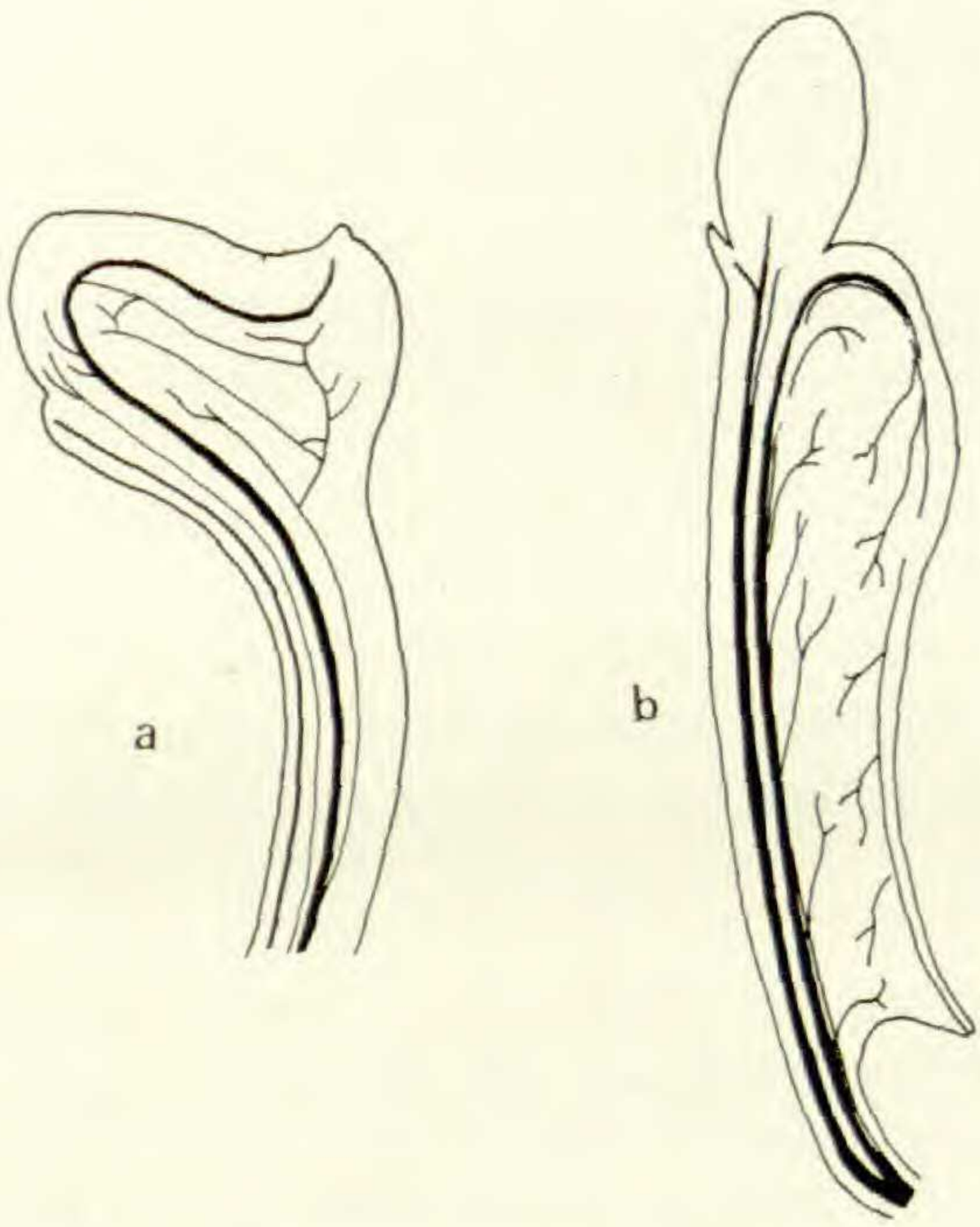

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FIGURE 8, above. Four diagrams to represent the transitions in form of the developing nectaries of *Marcgravia sintenisii.*

FIGURE 9, below. *Marcgravia rectiflora.* a. A young nectary-bearing pedicel showing the paired vascular strands, one to the aborted flower bud, the other showing the recurved path associated with invagination of the bract. b. A diagram of the vascular pattern found in the clone of *Marcgravia rectiflora* showing the early departure of the vascular supply to the nectary-bract, contrasted with the vascular supply to the normal bract and the flower bud.

rowed to a neck in the middle. The orifice is asymmetrical and the lip slightly recurved and pointed. The flowers number about nine to eleven and the nectary-bearing pedicels about four. The flowers are three to four times the size of those of *Marcgravia sintenisii* and shed the calyptrate corolla in a similar haphazard pattern, unassociated with the position of the flower on the inflorescence axis. Again, the stigmatic area was glistening and possibly receptive when the corolla-cap fell. The stamens also

spread widely, but the anthers shriveled within a few hours and became dark brown. The filaments were easily detached.

The position of the nectaries of *Marcgravia rectiflora* in relation to the flowers is such that pollination can not be effected by a hovering hummingbird in the theoretical manner but could occur in the way that Belt described birds acquiring pollen on their breasts from erect flowers. In fact no hummingbirds or todies were seen to visit the inflorescences of *M. rectiflora* in the course of many hours of observation. The bananaquit, however, was a frequent visitor, here landing in the middle of the inflorescence, forcing its way to the recurved nectary-bearing pedicels, and tipping its beak into the nectary. The bananaquits also managed to tear the nectaries from the orifice to the base, laying open the glandular tissue, or literally removing the globular end of the nectary. In the process of this activity the bananaquits brushed against many of the open flowers, and stamens were dispersed in all directions. It is possible that cross-pollination between newly opened flowers could be effected in this manner. Subsequently, bees which visited the inflorescence took advantage of the injured nectaries and approached the damaged tissue area directly from well below the flowers. In contrast to those of *Marcgravia sintenisii*, the nectaries of *M. rectiflora* do not develop a brilliant color but remain green and brown.

Bees, wasps, and hornets which visited the young inflorescences of *Marcgravia rectiflora* did not approach the cluster of flowers from above but landed below the flowering pedicels and worked their way up the axis to the nectary glands. In many cases the bees, wasps, and hornets did not bother with the nectary orifice but confined their feeding to the "corky" excrescences developed on the pedicels or on the outer surface of the saccate nectary.

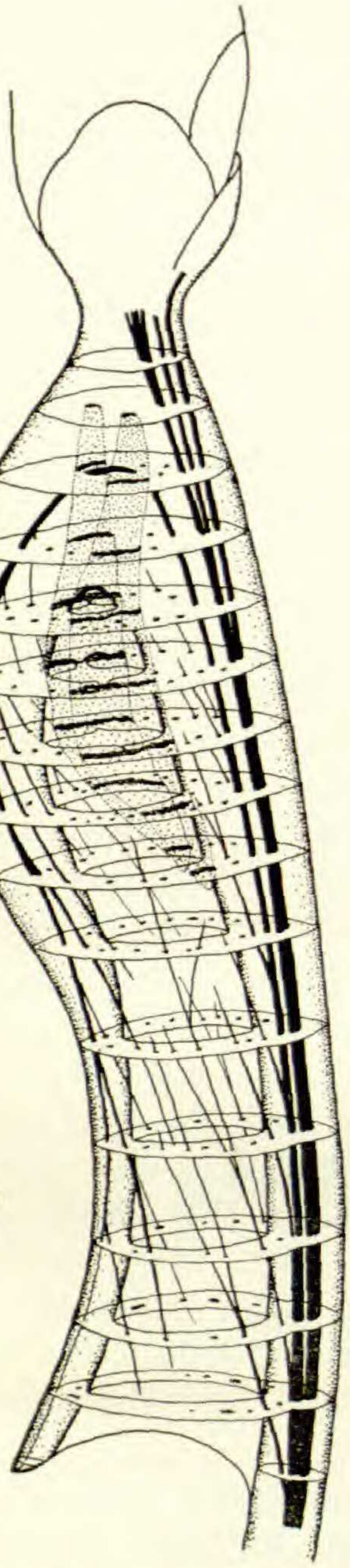
During the course of frequent observations it was noted that the hanging axillary branch and the inflorescence of *Marcgravia rectiflora* were the preferred territory of an anolid lizard (*Anolis evermanni*), which spent many hours on successive days in the middle of the inflorescence, but scrambled back up the stem at times while foraging. Like the bananaquit, the lizard was seen to crawl over open flowers and to break off stamens. It is interesting to speculate that a few flowers of *Marcgravia rectiflora* were pollinated by an anolid lizard. The anolid found the inflorescence a good hunting area and was seen to catch small insects apparently approaching the flowers. On one occasion the anolid caught a butterfly, but the other insects remain unidentified.

Mr. Henry Draper, with the aid of a telephoto lens, was able to record an anolid lizard with its snout in the orifice of one of the nectaries. Again the lizard probably was not supping on the nectar but catching small red-brown ants and mites which have been found within the nectaries in subsequent dissection. The lizard was missing from his favorite territory one afternoon when I planned to watch his behavior again. Nearly an hour of observation time passed before I realized that his usual haunt was then occupied by a snake (*Alsophis portoricensis* or *Dromicos exiguus*). This

snake was stretched along the full length of the branch and its head was in the center of the inflorescence. Neither the snake nor the lizard was seen on this branch in succeeding days.

I. W. Bailey (1922) observed the flowering characteristics of several species of *Marcgravia* in British Guiana and found that bagged inflorescences set fruit, as did some stems that flowered under water. The natural fertility of the two species in Puerto Rico was also high. Several inflorescences that were covered tightly with bags of cheese cloth during the summers of 1966 and 1967 produced developing fruit on as high a percentage of the flowers as did unbagged inflorescences. Swamy (1948) supported Bailey's observation that the anthers of *Marcgravia* split and release pollen grains before flower anthesis. He also noted that a large percentage of the pollen had germinated at anthesis and that pollen tubes of varying length were found. Some pollen tubes were observed on pollen collected from open flowers of both species occurring in Puerto Rico. It seems unlikely that pollen grains which had developed pollen tubes could be transported any distance in the process of cross-pollination. Swamy reiterated Bailey's conclusion that the two species they studied were autogamous or self-pollinated. This seems to be true of the two species studied in Puerto Rico, *M. sintenisii* and *M. rectiflora*. In both species the anthers were open and pollen was shed within the bud before the calyptrate corolla had fallen. The stigmatic area, however, did not appear to be receptive until after the loss of the corolla, at which time it was glistening and covered with adhering pollen. Recently Meeuse (1961) suggested that *Marcgravia* may be pollinated by bats. No bats have been observed in the Pico del Oeste area by the individuals who participated in that study. Although the participants spent relatively few nights in this cloudy and cool area, it is hard to believe that bats would do so either. There are bats in the area where *Marcgravia rectiflora* was studied, and a reasonable attempt was made to observe the few open flowers of *M. rectiflora* in the predawn and late evening hours. No bats were seen to visit the inflorescences under observation.

Bailey pointed out in 1922, "There has been considerable speculation concerning the origin and morphological significance of these nectariferous appendages. Are they metamorphosed bracteoles, abnormal pedicels, modified bracts, or appendages *sui generis*? Most recent students of the Marcgraviaceae have accepted Planchon and Triana's (1863) conclusion that they are evaginated bracts. It must be admitted that there is considerable evidence in favor of this view." He then noted, as had Goebel (1905), that "the concave or inner surface of the nectariferous appendages is the morphological equivalent of the under surface of the leaves. The outlets or pores of the hypophyllous glands are located in this dorsal surface and, accordingly, discharge their sugary excretions into the concavities of the bracts." However, Bailey also concluded, "That the nectaries of Marcgravia are not abnormal pedicels, as maintained by Seemann (1870), but are compound structures resulting from the fusion of a nectariferous bract and a sterile pedicel, is indicated, not only by their



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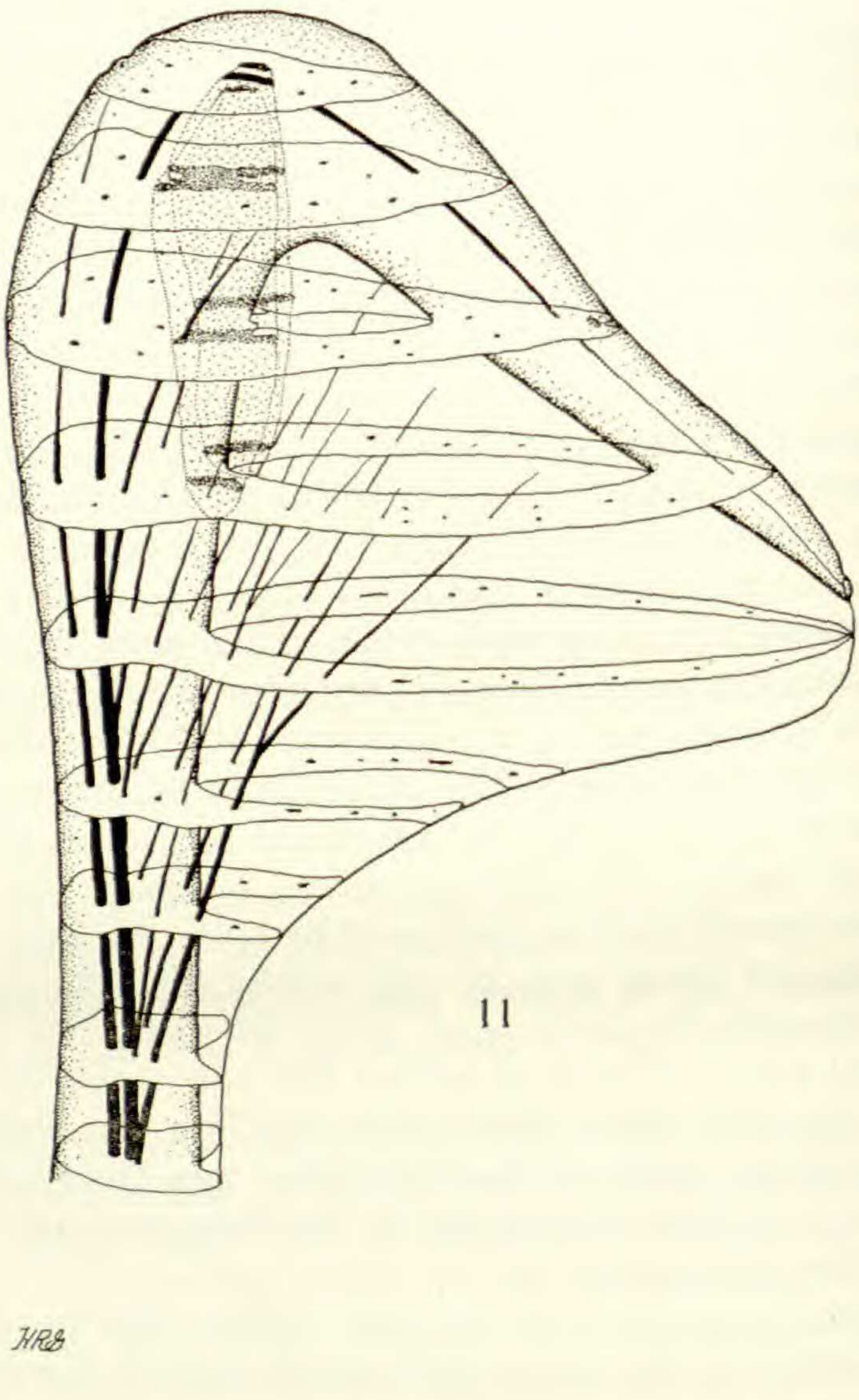

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FIGURE 10, left. A diagrammatic reconstruction of the nectary-bearing pedicel of the clone of *Marcgravia rectiflora* which develops a flower bud. Preparation was made from cleared pedicels and from transverse sections. Two elongated hypophyllous glands are evident. The secondary vascular supply to the nectary area is derived from the full length of the bundle which ascends, curves over, and descends into the outer area of the flask-shaped nectary. The absence of a bract above the nectary contrasts with the presence of the opposing bract.

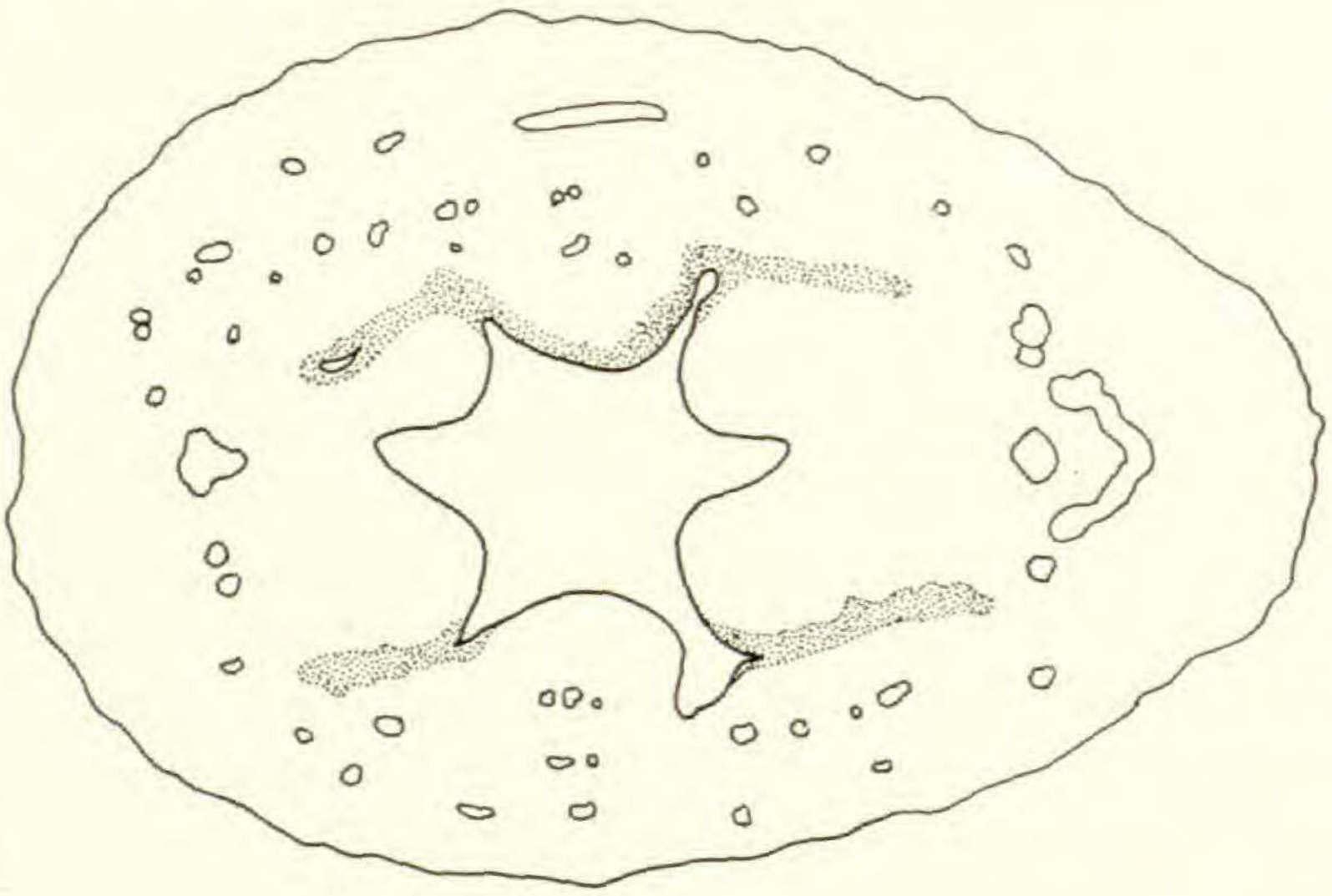
FIGURE 11, right. The galeate nectary of *Marcgravia sintenisii* diagrammatically reconstructed from cleared nectaries and from transverse sections. The small vascular strand to the aborted flower bud is shown. An ascending trace with secondary branches curves at the top of the nectary before descending to the morphological apex of the bract where a rudiment of the apical gland is shown. The flattened nectary has a wide orifice. Glandular tissue and its orifice are shown.

external morphology, but also by their internal anatomy." Bailey found "two distinct systems of fibro-vascular bundles in the nectaries, one belonging to the sterile pedicel and the other to the adnate bract." This statement is not completely accurate when applied to the two species used in the current study.

The floral structure of the two species of *Marcgravia* studied in Puerto Rico shows a calyx consisting of two pairs of overlapping, decussate sepals subtended and appressed by two smaller bracts (FIGURES 6, 7). In the flowering pedicel the vascular traces to these appendages depart from the central stele at about the same level and immediately below the vascular bundles which supply the corolla, androecium, and gynoecium. In the nectary-bearing pedicels, however, the flower is usually aborted and represented only by a small rudiment which has a very reduced vascular supply (FIGURES 8c, 9a). The bulk of the vascular tissue is directed to the nectary with the median bundle arching over at the apex of the nectary and descending to the lip and its terminal gland (FIGURES 8–11). Branch traces depart from both sides along the full length of this bundle, branching as they diverge into the body of the nectary. The vascular pattern can be observed readily in cleared nectary-bearing pedicels of *Marcgravia rectiflora*. (FIGURES 9b, 10). Numerous branched idioblasts and sclereids develop early in the nectaries of *Marcgravia sintenisii*, and in such profusion that only the main vascular bundles can be seen.

The secretive tissue is developed extensively in these nectaries. Bailey suggested that these were comparable to the hypophyllous glands found on the leaves, and the present observations support this conclusion. Two extensive areas of secretive tissue open through two pores in *Marcgravia rectiflora* (FIGURES 10, 12). Additional areas of secretory tissue, each with pores opening internally to the cavity, have been found in the nectaries of *M. sintenisii* (FIGURE 13).

The presence of rudimentary flowers at the apex of the pedicels which also bear the saccate nectaries has been noted frequently. Both Wittmack and Bailey illustrate pedicels in which the flower is of significant size and in some cases separated by a respectable distance from the nectary. One clone of *Marcgravia rectiflora* found and observed in Puerto Rico had well-developed flowers at the ends of nectary-bearing pedicels (FIGURES 6, 9, 10). The vasculature and glandular tissue of a nectary of this plant is illustrated (FIGURE 10). This clone was observed many times over a period of three years and there was no variation in the production of large flower buds. During development the flowers of the nectary-bearing pedicels and those without nectaries progressed at comparable rates until each was about two-thirds the mature size. At this point the flowers with subtended nectaries failed to increase further. The regular flowers enlarged, the corolla was shed, and fruit was set. The nectary-bearing pedicels fell off without the terminal flowers maturing or shedding the corolla. Examination of the flowers subtended by nectaries showed normal floral structure with well-developed stamens, the anthers of which contained mature pollen grains. When these structures were cleared and



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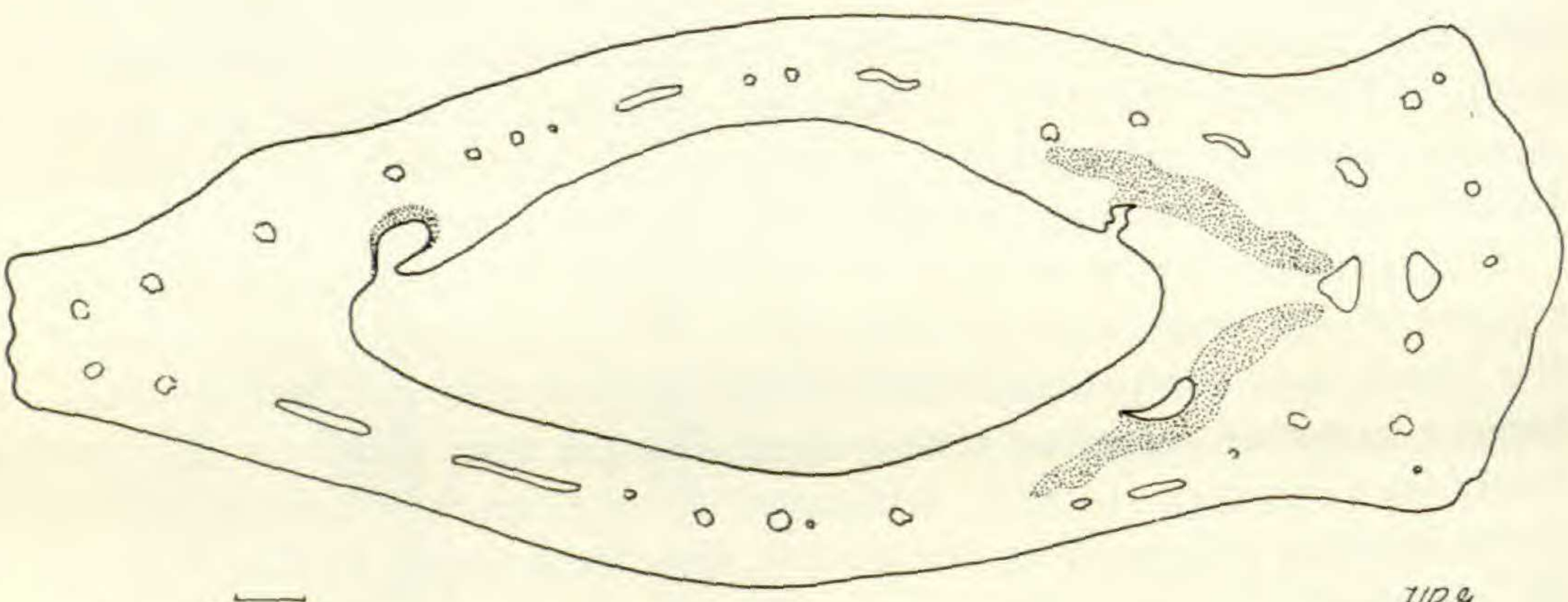

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FIGURE 12, above. A median transverse section of the nectary-bearing pedicel of *Marcgravia rectiflora* showing the opening into the cavity.

FIGURE 13, below. A median transverse section of the nectary-bearing pedicels of *Marcgravia sintenisii*. Three areas of glandular tissue are shown.

the vascular structure was examined, it was evident, as shown in the diagram (FIGURE 10), that a major vascular supply extended to the flower and that a branch of this system departed early, ran parallel to it, and ascended into the nectary area. This was conspicuous in contrast to nectary-bearing pedicels with abortive flowers where the vascular supply to the nectary surpassed in volume the vascular supply to the aborted flower. In each of the types of pedicels a single unit of vascular stele was present at the base of the pedicel, and the vascular supply to the nectary or the bract was but a branch of this central stele.

The normal flower of both species of *Marcgravia* has a four-parted calyx closely subtended by two bracts. The pedicels which bear nectaries, by contrast, possess but one normally developed bract opposite the

nectary area (FIGURE 10). The conclusion of Planchon that the nectary is a development of one of the bracts is verified. Although Planchon suggested this as an evaginated bract, the vocabulary of "fusion" or "adhering" remains in the literature. We have been able to examine a series of inflorescences of increasing age. FIGURES 2, 3, 8, and 9 show the adjustment in form that takes place in the maturation of the nectaries of both *M. rectiflora* and *M. sintenisii*. The distortion of form is gradual but consistent, leading to the respective saccate and galeate mature nectaries. The development pattern observed also supports the Planchon description of an invagination of one of the bracts which involves a distortion of the major part of the pedicel.

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ARNOLD ARBORETUM
HARVARD UNIVERSITY